



Year: 2015

The effects of foundation species on community assembly: a global study on alpine cushion plant communities

Kikvidze, Zaal ; Brooker, Robin W ; Butterfield, Bradley J ; Callaway, Ragan M ; Cavieres, Lohengrin A ; Cook, Bradley J ; Lortie, Christopher J ; Michalet, Richard ; Pugnaire, Francisco I ; Xiao, Sa ; Anthelme, Fabien ; Björk, Robert G ; Cranston, Brittany H ; Gavilán, Rosario G ; Kanka, Róbert ; Lingua, Emanuele ; Maalouf, Jean-Paul ; Noroozi, Jalil ; Parajuli, Rabindra ; Phoenix, Gareth K ; Reid, Anya ; Ridenour, Wendy M ; Rixen, Christian ; Schöb, Christian

Abstract: Foundation species can change plant community structure by modulating important ecological processes such as community assembly, yet this topic is poorly understood. In alpine systems, cushion plants commonly act as foundation species by ameliorating local conditions. Here, we analyze diversity patterns of species' assembly within cushions and in adjacent surrounding open substrates (83 sites across five continents) calculating floristic dissimilarity between replicate plots, and using linear models to analyze relationships between microhabitats and species diversity. Floristic dissimilarity did not change across biogeographic regions, but was consistently lower in the cushions than in the open microhabitat. Cushion plants appear to enable recruitment of many relatively stress-intolerant species that otherwise would not establish in these communities, yet the niche space constructed by cushion plants supports a more homogeneous composition of species than the niche space beyond the cushion's influence. As a result, cushion plants support higher α -diversity and a larger species pool, but harbor assemblages with lower β -diversity than open microhabitats. We conclude that habitats with and without dominant foundation species can strongly differ in the processes that drive species recruitment, and thus the relationship between local and regional species diversity.

DOI: <https://doi.org/10.1890/14-2443.1>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-112189>

Journal Article

Published Version

Originally published at:

Kikvidze, Zaal; Brooker, Robin W; Butterfield, Bradley J; Callaway, Ragan M; Cavieres, Lohengrin A; Cook, Bradley J; Lortie, Christopher J; Michalet, Richard; Pugnaire, Francisco I; Xiao, Sa; Anthelme, Fabien; Björk, Robert G; Cranston, Brittany H; Gavilán, Rosario G; Kanka, Róbert; Lingua, Emanuele; Maalouf, Jean-Paul; Noroozi, Jalil; Parajuli, Rabindra; Phoenix, Gareth K; Reid, Anya; Ridenour, Wendy M; Rixen, Christian; Schöb, Christian (2015). The effects of foundation species on community assembly: a global study on alpine cushion plant communities. *Ecology*, 96(8):2064-2069.

DOI: <https://doi.org/10.1890/14-2443.1>

The effects of foundation species on community assembly: a global study on alpine cushion plant communities

ZAAL KIKVIDZE,^{1,25} ROBIN W. BROOKER,² BRADLEY J. BUTTERFIELD,³ RAGAN M. CALLAWAY,⁴
LOHENGRIN A. CAVIERES,⁵ BRADLEY J. COOK,⁶ CHRISTOPHER J. LORTIE,⁷ RICHARD MICHALET,⁸
FRANCISCO I. PUGNAIRE,⁹ SA XIAO,¹⁰ FABIEN ANTHELME,¹¹ ROBERT G. BJÖRK,¹² BRITTANY H. CRANSTON,¹³
ROSARIO G. GAVILÁN,¹⁴ RÓBERT KANKA,¹⁵ EMANUELE LINGUA,¹⁶ JEAN-PAUL MAALOUF,¹⁷ JALIL NOROOZI,¹⁸
RABINDRA PARAJULI,¹⁹ GARETH K. PHOENIX,²⁰ ANYA REID,²¹ WENDY M. RIDENOUR,²² CHRISTIAN RIXEN,²³
AND CHRISTIAN SCHÖB²⁴

¹4-D Research Institute, Ilia State University, 5 Cholokashvili Avenue, Tbilisi 0162 Georgia

²The James Hutton Institute, Craigiebuckler, Aberdeen AB15 8QH Scotland, United Kingdom

³Merriam-Powell Center for Environmental Research, Northern Arizona University, P.O. Box 6077, Flagstaff, Arizona 86011 USA

⁴Division of Biological Sciences and the Institute on Ecosystems, University of Montana, Missoula, Montana 59812 USA

⁵Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción,
Casilla 160-C, Concepción, Chile

⁶Department of Biological Sciences, Minnesota State University, Mankato, Minnesota 56001 USA

⁷Department of Biology, York University, 4700 Keele Street, Toronto, Ontario M3J 1P3 Canada

⁸University Bordeaux, UMR CNRS 5805 EPOC, 33405 Talence, France

⁹Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, EEZA-CSIC, Carretera de Sacramento s/n,
La Cañada de San Urbano, E-04120 Almería, Spain

¹⁰MOE Key Laboratory of Cell Activities and Stress Adaptations, School of Life Sciences, Lanzhou University,
Lanzhou 730000 China

¹¹Institut de Recherche pour le Développement (IRD), UMR DIADE/AMAP, CIRAD, TA A51/PS2,
Montpellier Cedex 5, 34398 France

¹²Department of Earth Sciences, University of Gothenburg, P.O. Box 460, SE-405 30 Gothenburg, Sweden

¹³Department of Botany, University of Otago, P.O. Box 56, Dunedin, New Zealand

¹⁴Departamento Biología Vegetal II, F. Farmacia, Universidad Complutense, E-28040 Madrid, Spain

¹⁵Institute of Landscape Ecology, Slovak Academy of Science, Štefánikova 3, Bratislava 814 99 Slovakia

¹⁶Reperto TeSAF, Vialledell'Università, 16, 35020 Legnaro, Pd, Italy

¹⁷University Bordeaux, UMR CNRS 5805 EPOC, 33405 Talence, France

¹⁸Department of Plant Biology, Faculty of Natural Science, University of Tabriz, Tabriz 51666 16471 Iran

¹⁹Central Department of Botany, Tribhuvan University, Kirtipur, Kathmandu, Nepal

²⁰Department of Animal and Plant Sciences, The University of Sheffield, Western Bank, Sheffield S10 2TN United Kingdom

²¹Department of Forest and Conservation Sciences, University of British Columbia, 2621 – 2424 Main Mall,
Vancouver, British Columbia V6T 1Z4 Canada

²²Biology Department, University of Montana Western, Dillon, Montana 59725 USA

²³Community Ecology, WSL Institute for Snow and Avalanche Research SLF, Flüelastrasse 11, Davos CH-7260 Switzerland

²⁴Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190,
CH-8057 Zürich, Switzerland

Abstract. Foundation species can change plant community structure by modulating important ecological processes such as community assembly, yet this topic is poorly understood. In alpine systems, cushion plants commonly act as foundation species by ameliorating local conditions. Here, we analyze diversity patterns of species' assembly within cushions and in adjacent surrounding open substrates (83 sites across five continents) calculating floristic dissimilarity between replicate plots, and using linear models to analyze relationships between microhabitats and species diversity. Floristic dissimilarity did not change across biogeographic regions, but was consistently lower in the cushions than in the open microhabitat. Cushion plants appear to enable recruitment of many relatively stress-intolerant species that otherwise would not establish in these communities, yet the niche space constructed by cushion plants supports a more homogeneous composition of species than the niche space beyond the cushion's influence. As a result, cushion plants support higher α -diversity and a larger species pool, but harbor assemblies with lower β -diversity than open microhabitats. We conclude that habitats with and without dominant foundation species can strongly differ in the processes that drive species recruitment, and thus the relationship between local and regional species diversity.

Key words: β -diversity; biodiversity; biogeographic gradients; community assembly rules; cushion plants; foundation species; niche construction; species recruitment.

INTRODUCTION

Manuscript received 23 December 2014; revised 27 March 2015; accepted 1 April 2015. Corresponding Editor: P. M. Kotanen.

²⁵ E-mail: zaal.kikvidze@iliauni.edu.ge

Foundation species can structure ecosystems by modulating ecological processes (Ellison et al. 2005) particularly through constructing ecological niche space,

an ability that is crucial to understand ecosystem patterns and processes (Matthews et al. 2014). One of the most important ecological processes influenced by foundation species is community assembly (Callaway 2007, Loreau et al. 2013), though such effects are poorly understood (Schöb et al. 2012). An analysis of the effects of foundation species on community assembly can be conducted in a study system where two microhabitats, one dominated by a foundation species and another habitat out of the influence of the foundation species, co-occur in the same physical environment (Schöb et al. 2012). Using such two-phased study systems, investigations over large spatial scales can help understand community assembly (Qian and Ricklefs 2007, Brooker et al. 2009, Kraft et al. 2011) and elucidate the effects of foundation species (Butterfield et al. 2013, Cavieres et al. 2014). Here we report on a study of this kind that was undertaken in alpine communities dominated by species with cushion morphologies.

In alpine systems, plants with a highly compact, low-growing, mat-forming morphology are called “cushion species” (Aubert et al. 2014). While not representative of all alpine systems, these cushion-dominated communities occur globally across many alpine and arctic environments (e.g., Körner 2003, Aubert et al. 2014). Cushion plants can stabilize and ameliorate abiotic conditions (Frenot et al. 1998), improve soil nutrient content (Anthelme et al. 2012), enhance the arbuscular mycorrhizal status of associated plant species (Casanova-Katny et al. 2011), and increase the abundance and diversity of pollinators (Reid and Lortie 2012, Liczner and Lortie 2014). These systems allow for a comparison of two contrasting microhabitats: a relatively benign microhabitat inside cushions where many drought- and cold-intolerant species occur, and a relatively severe microhabitat in the open areas surrounding cushions that is colonized at low densities by other stress-tolerant species (Cavieres et al. 2014).

One approach to understanding community assembly processes, and the one we use here, involves the analysis of species distributions across sampled plots within a community (Chase et al. 2011, Kraft et al. 2011). In our study, this involves comparing variation in species composition among replicate plots within each of the contrasting microhabitats. We ask: what are the effects of foundation species on species richness within plots (α -diversity), on the variation in species compositions across plots within sites (β -diversity) and on the species pool of sites? Cushion plants have been shown to increase species diversity (Schöb et al. 2012, Butterfield et al. 2013, Cavieres et al. 2014) probably through stress amelioration and disturbance moderation, relaxing the local environmental filters that operate in the neighboring open microhabitat (Schöb et al. 2012, Cavieres et al. 2014). Yet, these facilitative effects might result in increased similarity of species compositions among the plots within the cushion microhabitat, as compared to those in the open areas, because the same facilitated

species can associate with many of the cushions (and so will be present in many of the cushion plots) owing to the construction of similar niches by the cushions (McIntire and Fajardo 2009). On the other hand, morphological variation between different species of cushions, among cushions of a given species, and within individual cushions, can also create multiple niches, thereby increasing environmental heterogeneity (Schöb et al. 2012, 2013, McIntire and Fajardo 2014). Such heterogeneity could increase floristic dissimilarity among cushion-associated plants and counterbalance their diversity-dampening environment-moderation effect. In summary, more than a single potential alternative exists regarding the effects of cushions on community assembly. We explored how cushion species can change community assembly processes by comparing diversity patterns among cushion microhabitats vs. among open microhabitats across 83 cushion plant communities on five continents. We also measured soil organic matter and soil moisture in a smaller subset of sites to assess the extent to which contrasting diversity patterns in cushions and open areas reflected the patterns of variation in the physical environment experienced by plants.

MATERIALS AND METHODS

Details of data collection are presented by Cavieres et al. 2014, and in Appendix A. In brief, we studied 83 alpine plant communities (sampling sites) in North and South America, Europe, Asia, and New Zealand. At each site, we recorded vascular plant species within paired plots consisting of a single cushion and an adjacent open plot of equal size to the cushion. Sampling sites we established on alpine scree soils with well-developed cushion plants in visibly advanced stage of successions. We therefore considered the studied cushion communities as “saturated” communities (see also Cavieres et al. 2014). Cushion plants were haphazardly selected within relatively homogenous habitats with respect to soils, elevation and aspect (Appendix A).

We calculated three characteristics for each site: (1) Local richness (α -diversity), which refers to the mean number of species found per plot in each microhabitat (the cushions or the open area plots) at each sampling site. (2) Microhabitat species pool, which refers to the extrapolated species richness in each microhabitat at each sampling site. The total observed species richness of the assumedly saturated communities per microhabitat and site was complemented by the estimated number of unseen species using the Chao estimator in specpool, a function of the vegan library (Oksanen et al. 2013). (3) Sørensen's multi-site dissimilarity index (β -diversity). This is based on Sørensen's classic index (Baselga and Orme 2012). It uses presence/absence data, and measures the dissimilarity in floristic composition between each pair of plots. The values of β -diversity vary between 0 and 1 and are higher the more dissimilar the

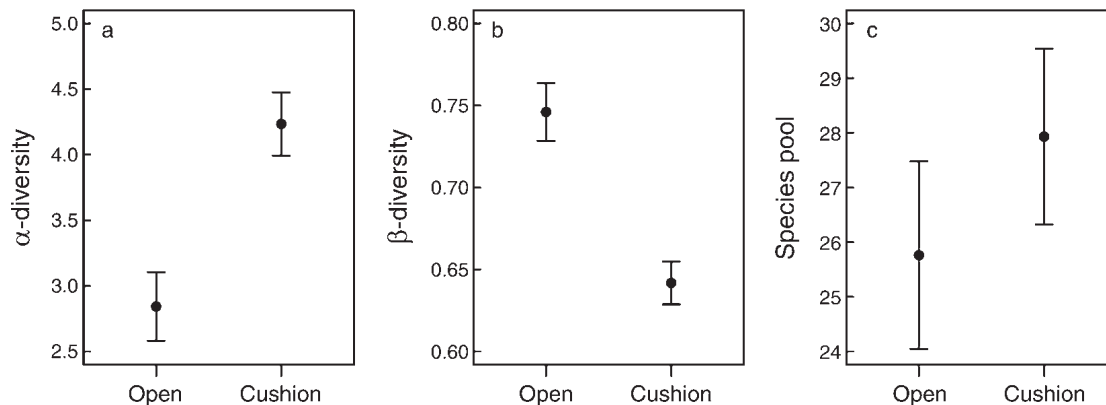


FIG. 1. Diversity partitioning in cushion and open microhabitats of alpine scree slopes: (a) observed α -diversity per plot, (b) β -diversity quantified as Sørensen's multi-site dissimilarity index, (c) species pool quantified as the extrapolated species pool (number of species) per microhabitat. Values displayed are global means \pm SE.

plant assemblages are. We used the function `beta.multi` from the software package `betapart` to calculate Sørensen's dissimilarity index. We also used other measures of β -diversity such as Raup-Crick dissimilarity and β deviation (Kraft et al. 2011). The results were similar to those of Sørensen's and we report here the results only with Sørensen's index. The results with other indices are shown in Appendix B.

Soil samples were taken within paired plots from beneath cushions and in open areas at a subset of 15–20 sites (Appendix A). Samples were kept in sealed containers and fresh mass was determined immediately after sampling in the field. Soil moisture (percentage of fresh soil) was determined by mass loss after drying the samples at 105°C for 48 h, soil organic matter content (SOM, percentage of dry soil) was determined by mass loss after ignition at 400°C for 20 h (Schöb et al. 2012). For further analyses, we used the mean and the coefficient of variation of soil moisture and SOM as measures of environmental severity of the microhabitats and environmental heterogeneity among plots within a microhabitat, respectively.

Nonparametric paired tests (Wilcoxon signed rank tests) were used to test for differences between cushion and open microhabitats for indices of α - and β -diversity, the species pool, and the mean values and their variation (CV) for soil moisture or SOM. Due to strong collinearity between α -diversity and the species pool ($r = 0.67$), separate linear mixed models were performed to test the relationships of α -diversity and the species pool on β -diversity, including the microhabitat type and its interactions with either α -diversity or the species pool as additional predictor variables and the sites as random variable. The effect of mean and variation in soil moisture and SOM on β -diversity, and their interactions with the microhabitat type was tested similarly, i.e., with separate linear mixed models that included the sites as random effect. Again, separate analyses were performed due to the high collinearity between mean SOM and mean soil moisture ($r = 0.84$). For the latter analysis,

and due to the small sample size, unimportant variables were eliminated using the procedure of step-wise selection based on Akaike's information criterion (AIC) using the maximum likelihood estimation. The variables remaining in the selected model were then analyzed using type-I ANOVA based on a model fitted with restricted maximum likelihood estimation. Statistical analyses were done in the R environment (R Core Team 2013).

RESULTS

The α -diversity was, on average, 1.39 species higher in cushions compared to the open plots (sum of positive ranks $V = 3112$, $P < 0.001$; Fig. 1a). Similarly, the estimated species pool was 2.17 species higher in cushions compared to the open microhabitat ($V = 2260$, $P = 0.005$, Fig. 1c). In contrast, β -diversity was on average 0.10 units lower in cushions compared to open microhabitats ($V = 314$, $P < 0.001$; Fig. 1b).

The β -diversity was significantly related to α -diversity and species pool, and the microhabitat type (Fig. 2). There was a significant interaction between the microhabitat type and α -diversity explaining β -diversity, whereas the effect of species pool on β -diversity was independent of the microhabitat type (Table 1). Overall, the relationship between α -diversity and β -diversity ($r = -0.63$) was much stronger than the relationship between species pool and β -diversity ($r = -0.14$). The relationship between α -diversity and β -diversity was stronger for the open microhabitat ($r = -0.67$) compared to the cushion microhabitat ($r = -0.48$).

Mean soil moisture was significantly higher in cushions ($23\% \pm 5\%$ [mean \pm SE]) compared to the open area plots ($17\% \pm 6\%$; $V = 186$, $P = 0.001$). Likewise, mean SOM was higher in cushions ($10.7\% \pm 3.4\%$) compared to open areas ($3.9\% \pm 0.4\%$; $V = 120$, $P < 0.001$). Coefficients of variation in soil moisture (cushion, 36 ± 3 ; open, 38 ± 3) and SOM (cushion, 35 ± 5 ; open, 37 ± 5) showed nonsignificant differences among microhabitats ($P > 0.38$). The stepwise selection

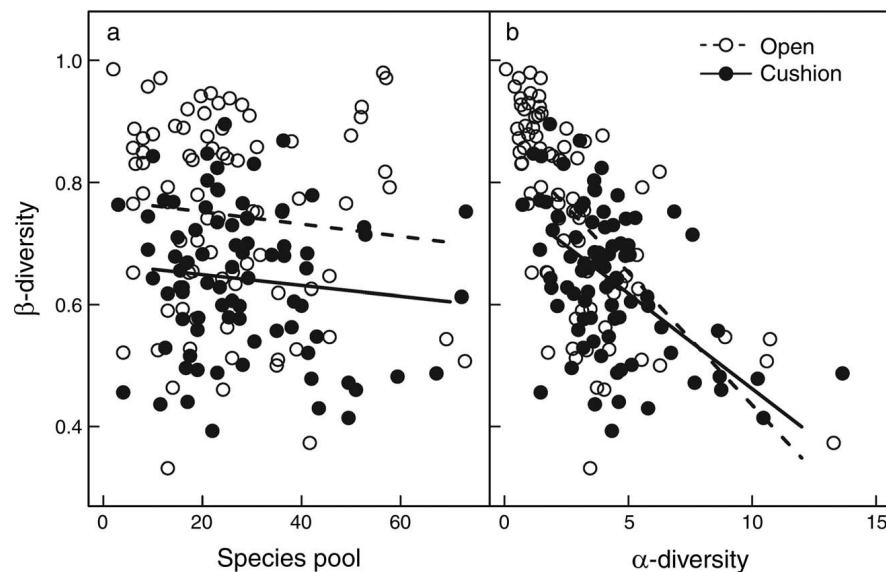


FIG. 2. The global relationships of (a) the species pool and (b) α -diversity with β -diversity in cushion and open microhabitats of alpine scree slopes. Plots include the value of diversity indices for each site and microhabitat (dots) and model estimated means for each microhabitat (lines).

procedure selected all variables relating soil moisture to β -diversity, whereas a reduced model without the interaction terms of mean SOM \times microhabitat, and mean SOM \times CV SOM was selected for the relationship between SOM and β -diversity. Overall, higher mean soil organic matter reduced β -diversity with no significant differences in this relationship among microhabitats, whereas higher mean soil moisture differently affected β -diversity in the two microhabitats, i.e., it tended to reduce β -diversity in cushions and to increase β -diversity in the open (Table 2). Variation in soil moisture and SOM were only marginally significantly related to β -diversity (Table 2): CV in soil moisture tended to increase with increasing β -diversity independently of the habitat type, whereas CV in SOM tended to increase with increasing β -diversity only in the open area.

TABLE 1. Statistical results of linear mixed modeling of the relationship of α -diversity, species pool, microhabitat type, and its interaction terms with α -diversity and species pool.

Variable	df	F	P
Analysis of α-diversity			
(Intercept)	1, 82	3748	<0.001
α -diversity	1, 80	176.2	<0.001
Microhabitat	1, 80	19.47	<0.001
α -diversity \times Microhabitat	1, 80	6.779	0.011
Analysis of species pool			
(Intercept)	1, 82	2432	<0.001
Species pool	1, 80	5.14	<0.001
Microhabitat	1, 80	62.17	<0.001
Species pool \times Microhabitat	1, 80	0.019	0.890

Notes: Sites ($n = 83$) were included as a random variable. The sequence of variables for the type-I ANOVA is as presented in the table.

DISCUSSION

Community assembly is typically viewed as a hierarchical process with local species assemblages representing subsets of a larger species pool. These subsets are established by filtering through local abiotic and biotic factors such as microclimate, soil type, plant interactions, herbivores, and pollinators that thus determine the size and species composition of these subsets (Lortie et al. 2004, Götzenberger et al. 2012). These factors vary from one plot to another, thus producing certain levels of β -diversity or variation in species composition across plots. In our study, the consistently lower floristic

TABLE 2. Statistical results of linear mixed modeling of the relationships between the site-level means and coefficients of variation (CV) of either soil moisture (SM) or soil organic matter (SOM), and their interactions with microhabitat type.

Variable	df	F	P
Analysis of SM			
(Intercept)	1, 20	543	<0.001
Mean SM	1, 15	0.45	0.51
SM CV	1, 15	3.56	0.075
Mean SM \times SM CV	1, 15	0.44	0.52
Mean SM \times Microhabitat	1, 15	11.38	0.004
SM CV \times Microhabitat	1, 15	1.77	0.20
Analysis of SOM			
(Intercept)	1, 15	304	<0.001
Mean SOM	1, 12	10.49	0.007
SOM CV	1, 12	0.46	0.51
SOM CV \times Microhabitat	1, 12	3.54	0.084

Notes: Sites ($n = 20$ and $n = 15$ for SM and SOM, respectively) were included as a random variable. The sequence of variables for the type-I ANOVA is as presented in the table. The most parsimonious model selected out of the full model using Akaike's information criterion is shown.

dissimilarity found in the cushions vs. the open areas, coupled with the similar effect of species pool on β -diversity but a different effect of α -diversity on β -diversity between microhabitats, indicates markedly different assembly processes in these two types of microhabitat. Furthermore, β -diversity at the global scale was fairly strongly related to species pool, reflecting the inherent relationship between these two diversity measures beyond differences in community assembly processes (Kraft et al. 2011).

The idea that community assembly processes in cushions differ from those outside of the influence of these foundation species was first suggested by Schöb et al. (2012) for cushion plants in the Sierra Nevada Mountains in Spain. Their proposition is now supported by our global-scale study, allowing us to generalize concerning the effects of cushion foundation species on community assembly processes. First, cushions generally increased local species richness (and hence the microhabitat species pool) as compared to the open area plots (see also Butterfield et al. 2013, Cavieres et al. 2014). Second, floristic dissimilarity, i.e., β -diversity, among plots was generally lower in the cushions than in the open area plots as mentioned above. Third, the cushion microhabitat was characterized by higher soil moisture and SOM than the open microhabitat, indicating alleviated stress conditions in cushions. This stress and disturbance moderation is likely to be a part of the niche construction by cushion plants, allowing for recruitment of less stress-tolerant species (Liancourt et al. 2005, Schöb et al. 2012). This is supported by the study on leaf dry mass content (LDMC) and specific leaf area (SLA) of the plants associated with cushions, collected from a small subset of our sampling sites (four sites in southeast Spain); this study showed lower LDCM but higher SLA in cushion-associated plants thus indicating the better water availability for plants in the cushion microhabitat as compared to the open area (Schöb et al. 2012). Probably, the effect of environmental stress and disturbance moderation by cushions predominates over the variation in the physical environment within cushions, and the net result is reduced β -diversity. This is supported by the significant link between mean soil organic matter and β -diversity, but the weaker relationship between variation in soil moisture or SOM and β -diversity. Furthermore, when the relationship between the species pool and local (α) richness is linear and with a zero intercept, β -diversity gives an unbiased measure of niche width (Botta-Dukát 2012), as is the case in our study. Therefore, the lower β -diversity found in the cushions strongly suggests that the niche space constructed by the cushion plants is more homogeneous than that in the open area. In other words, the reduced β -diversity is most likely the result of an environmental filtering process selecting a certain subset of species for growth in cushions. These less stress/disturbance-tolerant species may benefit from the better growth conditions in cushions, irrespective of variation between

cushions in these growing conditions, and be responsible for the increased uniformity of species composition associated with the foundation species. Overall, cushion vegetation can be considered a distinct plant community.

We conclude that the habitats with and without dominant foundation species can dramatically differ in the processes that drive species recruitment and hence can influence strongly the relationship between local and regional species diversity (Michalet et al. 2014). The global scale of our study ensures generality of our findings at least for this class of foundation species: plants with a cushion morphology. A key question is whether similar patterns exist for other keystone facilitator growth forms, for example shrub species in semiarid environments.

ACKNOWLEDGMENTS

Z. Kikvidze acknowledges the support from the 4-D research program of the Ilia State University. R. W. Brooker was supported by grants from the Macaulay Institute and the James Hutton Institute. Swedish strategic research area Biodiversity and Ecosystem services in a Changing Climate (BECC) provided support to R. G. Björk. S. Xiao was supported by State Key Program of National Natural Science of China (31230014), National Natural Science Foundation of China (31070357, 40901019, 31000203 and 31000178), and Qilian Shan station of Glaciology and Ecological Environment. C. Schöb was financially supported by the Swiss National Foundation (PA00P3_136474 and PZ00P3_148261). F. I. Pugnaire was funded by the OAPN (grant 002/09) and MICINN (CGL2010-17081); L. A. Cavieres was funded by FONDECYT 1030821, 1060783, 358 1090389, FICM P05-002 and PFB-023. R. M. Callaway thanks the NSF EPSCoR Track-1 EPS-1101342 (INSTEP 3) for support. R. Kanka was funded to Slovak Research and Development Agency (project number APVV-0866-12). R. Michalet and J. P. Maalouf were funded by the CEDRE program 11EF8/L11 and the University of Bordeaux.

LITERATURE CITED

- Anthelme, F., B. Buendia, C. Mazoyer, and O. Dangles. 2012. Unexpected mechanisms sustain the stress gradient hypothesis in a tropical alpine environment. *Journal of Vegetation Science* 23:62–72.
- Aubert, S., F. Boucher, S. Lavergne, J. Renaud, and P. Choler. 2014. 1914–2014: a revised worldwide catalogue of cushion plants 100 years after Hauri and Schröter. *Alpine Botany* 124:59–70.
- Baselga, A., and C. D. L. Orme. 2012. Betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution* 3:808–812.
- Botta-Dukát, Z. 2012. Co-occurrence-based measure of species' habitat specialization: robust, unbiased estimation in saturated communities. *Journal of Vegetation Science* 23:201–207.
- Brooker, R. B., R. M. Callaway, L. A. Cavieres, Z. Kikvidze, C. J. Lortie, et al. 2009. Don't diss integration: a comment on Ricklefs's disintegrating communities. *American Naturalist* 174:919–927.
- Butterfield, B. J., L. A. Cavieres, R. M. Callaway, B. J. Cook, Z. Kikvidze, et al. 2013. Alpine cushion plants inhibit the loss of phylogenetic diversity in severe environments. *Ecology Letters* 16:478–486.
- Callaway, R. M. 2007. Positive interactions and interdependence in plant communities. Springer, Dordrecht, The Netherlands.

- Casanova-Katny, M. A., G. A. Torres-Mellado, G. Palfner, and L. A. Cavieres. 2011. The best for the guest: high Andean nurse cushions of *Azorella madreporica* enhance arbuscular mycorrhizal status in associated plant species. *Mycorrhiza* 21:613–622.
- Cavieres, L. A., et al. 2014. Facilitative plant interactions and climate simultaneously drive alpine plant diversity. *Ecology Letters* 17:193–202.
- Chase, J., N. J. B. Kraft, K. G. Smith, M. Vellend, and B. D. Inouye. 2011. Using null model to disentangle variation in community dissimilarity from variation in α -diversity. *Ecosphere* 2:24.
- Ellison, A. M., et al. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3: 479–486.
- Frenot, Y., J. C. Gloaguen, M. Cannavacciuolo, and A. Bellido. 1998. Primary succession on glacier forelands in the subantarctic Kerguelen Islands. *Journal of Vegetation Science* 9:75–84.
- Götzenberger, L., et al. 2012. Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biological Reviews* 87:111–127.
- Körner, C. 2003. *Alpine plant life—functional plant ecology of high mountain ecosystems*. Springer, Heidelberg, Germany.
- Kraft, N. J. B., et al. 2011. Disentangling the drivers of diversity along latitudinal and elevational gradients. *Science* 333:1755–1758.
- Liancourt, P., R. M. Callaway, and R. Michalet. 2005. Stress tolerance and competitive response-ability determine the outcome of biotic interactions. *Ecology* 86:1611–1618.
- Licznar, A. R., and C. J. Lortie. 2014. A global meta-analytic contrast of cushion-plant effects on plants and on arthropods. *PeerJ* 2:e265.
- Loreau, M., et al. 2013. Unifying sources and sinks in ecology and Earth sciences. *Biological Reviews* 88:365–379.
- Lortie, C., et al. 2004. Rethinking plant community theory. *Oikos* 107:433–438.
- Matthews, B., L. De Meester, C. G. Jones, B. W. Ibelings, T. J. Bouma, V. Nuutinen, J. van der Koppel, and J. Odling-Smee. 2014. Under niche construction: an operational bridge between ecology, evolution, and ecosystem science. *Ecological Monographs* 84:245–263.
- McIntire, E. J., and A. Fajardo. 2009. Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology* 90:46–56.
- McIntire, E. J. B., and A. Fajardo. 2014. Facilitation as a ubiquitous driver of biodiversity. *New Phytologist* 201:403–416.
- Michalet, R., et al. 2014. Competition, facilitation and environmental severity shape the relationship between local and regional species richness in plant communities. *Ecography* 38:335–345.
- Oksanen, J., et al. 2013. *vegan: community ecology package*. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>
- Qian, H., and R. E. Ricklefs. 2007. A latitudinal gradient in large-scale beta diversity for vascular plants in North America. *Ecology Letters* 10:737–744.
- R Core Team. 2013. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Reid, A. M., and C. J. Lortie. 2012. Cushion plants are foundation species with positive effects extending to higher trophic levels. *Ecosphere* 3:96.
- Schöb, C., C. Armas, M. Guler, I. Prieto, and F. I. Pugnaire. 2013. Variability in functional traits mediates plant interactions along stress gradients. *Journal of Ecology* 101:753–762.
- Schöb, C., B. J. Butterfield, and F. I. Pugnaire. 2012. Foundation species influence trait-based community assembly. *New Phytologist* 196:824–834.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: <http://dx.doi.org/10.1890/14-2443.1.sm>